14.—Disjunct plant distributions on the south-western Nullarbor Plain, Western Australia

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Abstract

Recent collections of plant specimens from several isolated dune systems on the coast of the Great Australian Bight between Point Culver and Twilight Cove, Western Australia, are discussed. These siliceous cliff-top dune systems are colonised by species regarded as typical of the "quonkan" (siliceous sand plain) of the south-west botanical province of Western Australia. These species are not found on the calcareous soils of the Nullarbor Plain. The disjunct distribution patterns of some species are considered to have resulted from disruption of a continuous vegetation belt that developed on the exposed sand deposits of the continental shelf, during the last period of marine regression, in the Late Pleistocene. Species similarities between south-eastern and south-western Australia are discussed in the context of these disjunct distribution patterns.

Introduction

Botanically, the Nullarbor Plain is defined as the tree-less (*nulla, arbor*) area on the limestone plain in central, southern Australia, north of the Great Australian Bight (Delisser 1867). The vegetation of the region consists of low scrub, dominated by members of the Chenopodiaceae (Willis 1959). However the extension of the use of the sobriquet to encompass the whole of the region containing the horizontally-bedded Miocene limestones has become a common practice* (Jennings 1963, Dunkley 1967, Parsons 1970). The restricted botanical region (Fig. 1) lies to the east of the areas discussed here, and has little bearing on this discussion.

In the south-western part of the limestone plateau, there are several isolated areas on or near the coast where the limestones are covered with younger deposits of aeolian calcarenite (Lowry 1970) and unconsolidated siliceous sand dunes. These 'sand patches' are situated at Point Culver, at Toolinna (north-west of Point Culver), south-west of Point Dover, and at Twilight Cove (Fig. 3 in Jennings 1967). Two of these areas, Toolinna and Twilight Cove (Fig. 2), have been visited by the author. On those occasions, plant specimens were collected, data on the vegetation recorded and soil samples obtained. Twilight Cove was visited in December 1972, August and October 1973, while Toolinna was visited only in October 1973. The visits were made in order to collect specimens for a taxonomic revision of *Adenanthos* Labill. (Proteaceae).

Some of the species collected on the sand patches had not previously been recorded east of Israelite Bay or Mount Ragged (Fig 2). These plants are regarded as typical members of the *quonkan** (Brooks 1894), or flora of the siliceous sand plain, that is found between Esperance and Israelite Bay. Their occurrence on these isolated dune systems presents an interesting phytogeographic problem, relating to the history of both land forms and vegetation in the areas adjacent to the Great Australian Bight.

Vegetation zones of south-western Australia

The South-West Botanical Province of Western Australia as defined by Diels (1906) is noted for the great diversity and the high rate of endemism that the flora exhibits (Burbidge 1960, Beard 1969, Marchant 1973). The province has been variously delimited, but generally covers a triangular-crescentic area bounded by the coast of Western Australia, and by a line extending from Shark Bay to Israelite Bay, corresponding approximately to the 175 mm winter isohyet (Gardner 1956) (Fig. 1). While most definitions of the region depend on climatic and botanical data (Marchant 1973), in certain areas it is possible to relate these data to geological information. Thus in the south-eastern region near Israelite Bay, the province terminates at the boundary between the rocks of the Precambrian Shield and the Tertiary sedimentary rocks of the Nullarbor Plain (Fig. 2).

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* Lowry (1970) used the name "Bunda Plateau" to cover this geological area as he considered the term "Nullarbor Plain" too useful to modify its original use. However common usage has already expanded the application of the name and as it is employed by Parsons (1970) in the widest sense, it is used herein to encompass the whole of the limestone region.

* This was spelt "quowcken" by Brooks, but should read "quonkan" (Mrs. A. E. Crocker, pers. comm.). *Quonkan* is an aboriginal name for the vegetation, composed mainly of low sclerophyll shrubs, that occurs on siliceous sand plain in this area (Brooks 1894). A similar word, "guangan", was used in areas north of Perth according to Drummond (Erickson 1969).

Beard (1973) has included the whole of the lowland plains, south of Point Culver, within the south-west province, as well as the region, underlain with limestone, that surrounds Mount Ragged and the Russell Range (Fig. 2). This latter area (Beard's "Cooper System") is placed in the South-West Interzone by Burbidge (1960), who also included most of the Eyre zone (Fig. 1) of the south-west province (Diels 1906) in that Interzone. Whatever the limits of these ill-defined zones and provinces, the areas under discussion are usually placed outside the south-west province within the Eremean province.

The flora of the south-west province is adapted to soil of extremely low fertility, and low calcium status (Seddon 1972), and some species may be extremely sensitive to changes in edaphic propensities (Diels 1906, Speck 1958).

Geology and geomorphology

The deposits of Miocene limestone that comprise the Nullarbor Plain (*sensu lat.*) extend from Mount Ragged in Western Australia, to Penong in South Australia (Fig. 1) and inland toward the Forrest Lakes and the Great Victoria Desert (Lowry and Jennings, 1974). Along the coast of the Great Australian Bight, there is an almost unbroken line of cliffs, about 80 m high, formed of horizontally-bedded limestones. There are a few areas of low-lying coastal plain, particularly the Roe Plains (Fig. 1) that disrupt this cliffed coastline.

Near Point Culver, the Baxter Cliffs swing inland to form the Wylie Scarp. A narrow coastal plain, the Israelite Plain (Lowry 1970) which is much lower than the main plateau of the Nullarbor (Fig. 2) lies between the Scarp and the coast. The Israelite Plain is composed of vegetated sand dunes with interdunal salt flats and lagoons. Lowry (1970) indicated that these dunes were deposited in the Pleistocene after the formation of the Wylie Scarp by marine erosion. At its northern end the dune systems converge on the emerged cliffs, and dunes found on the top of the cliffs, overlying the Miocene limestones (Jennings 1967), form the Point Culver sand patch (Fig. 2).

A similar situation is found at Twilight Cove. The lowland dune systems of the Roe Plains meet the cliffs where they swing inland to form the Hampton Range, and cliff-top dunes are situated on the plateau about 80 m above sea level (Jennings 1967). The Roe Plains sand deposits overlie a thin layer of Pleistocene calcarenite (Lowry 1970) and thus are probably late Pleistocene deposits, similar in age to those of the Israelite Plain.

Between Twilight Cove and Point Culver, to the south-west, the coastline is formed by the almost vertical Baxter Cliffs (Lowry 1970) which vary in height from 60 m to 100 m. At Toolinna there is no coastal lowland, but a dune system is isolated on top of the cliffs. A further small set

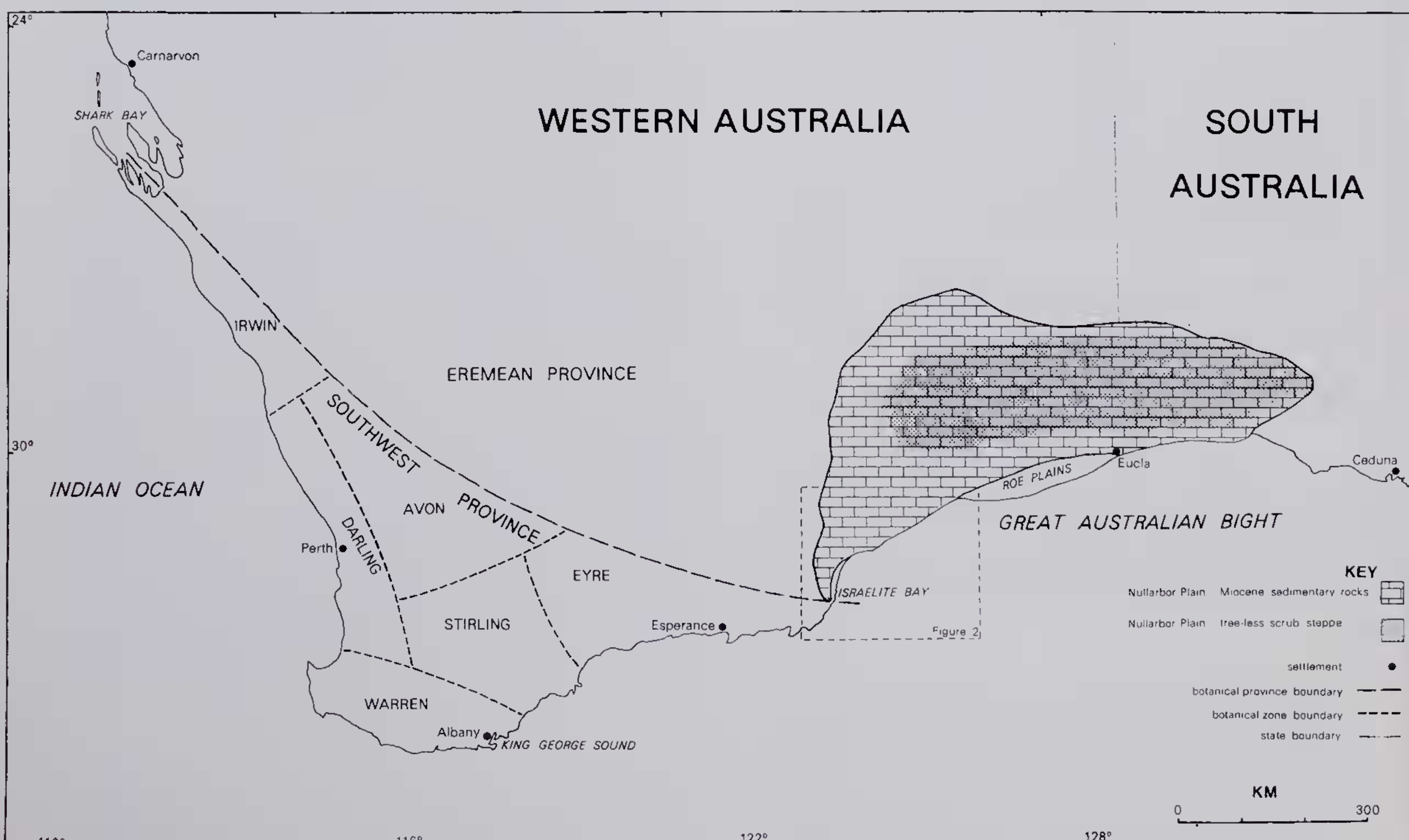

Figure 1.—South-western Australia, showing the relative extents of the tree-less scrub steppe and the Tertiary sedimentary deposits. The approximate boundaries of the botanical provinces and zones of Western Australia are indicated (Diels 1906, Gardner 1956).

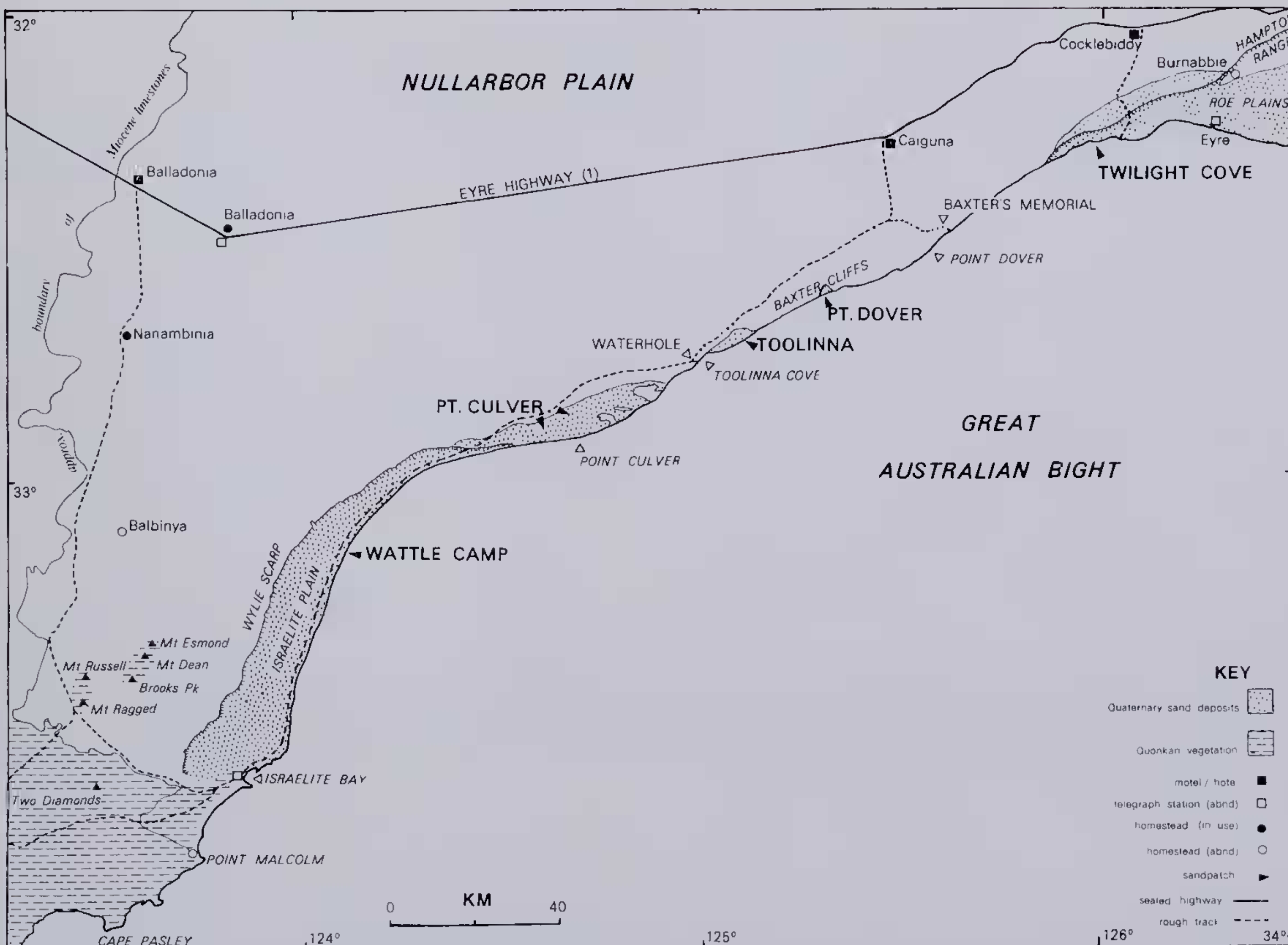

Figure 2.—South-western Nullarbor Plain showing the locations of the siliceous sand dunes discussed in the text.

of cliff-top dunes is isolated south-west of Point Dover*, between Toolinna and Twilight Cove. Again there is no associated coastal lowland (Jennings 1967). All the systems consist of sand deposits up to, or in some places more than 30 m deep.

Jennings (1967) suggested that these isolated dunes on the cliff tops were formed during a period of marine regression, when a very narrow coastal plain was exposed south-east of the present cliffs. The dunes could have been emplaced when ramps of wind-blown sand were formed against the cliffs, in a manner similar to the present situation at Point Culver and Twilight Cove. Subsequent marine transgression would have eroded away the ramps and isolated the deposits on the plateau. The maximum of last marine regression occurred during the late Pleistocene glacial period, about 20,000 years B.P., when sea levels were about 100 m lower than present datum (Jennings 1971). During that glacial period conditions suitable for dune emplacement would have occurred. These isolated sand patches could date from the late Pleistocene or early Holocene, though a greater age is possible if dunes were emplaced in previous glacial epochs (J. N. Jennings, pers. comm.). As the dunes at Point Culver and Twilight Cove are active and mobile at the present time, it is probable that dune emplacement will only take place when the coastal lowland south of the cliffs is very narrow; perhaps only a few kilometres wide. This dune building on the cliff-tops may not have taken place until sea levels were very close to the base of the Baxter Cliffs. This would mean that the deposits may be 10 000-6 000 years old. (Hydrographic charts for the coast in this region are incomplete. Several kilometres from the cliffs the ocean depth is about 40 m. Dates were derived using this depth and reconstructed sea-level curves for the Australian region (Thom and Chappell 1975).)

Jennings (1967), Lowry (1970) and Parsons (1970) indicate that there are aeolian calcarenite deposits underlying the sands at Twilight Cove and on the Roe Plains. Parsons (1970) stated that "sheet limestone" was encountered at 0.66 m in a profile at Twilight Cove. While Jennings (1967) stated that the dunes of the western Roe Plains, immediately adjacent to

* Jennings (1967, Fig. 4c) located this area about 2 km south-west of Point Dover at 32° 31′ S, 125° 30′ E. An examination of photomosaic maps revealed that the dunes are situated 32° 37′ S, 125° 15′ E about 30 km south-west of the point and nearer to Toolinna.

Table 1

*pH of soil and proportions of calcium carbonate in sand samples from cliff-top dunes.**

Sample number	Location	% $CaCO_3$ (ppm Ca^{++})	pH
TWS 1	dune surface ; on cliff top at Twilight Cove, before descending scarp, c.20 km south of Cocklebiddy	nil	5·7
TWS 2	as TWS 1	nil	5·9
TWC 3	1m below TWS 2, in profiile	nil	5·9
AFOR	dune surface ; about halfway through dune system at Twilight Cove, c.15 km south of Cocklebiddy	nil	5·6
AFOR 1	as AFOR	nil	5·7
HYB	as AFOR	nil	6·0
TOO 1	dune surface, Toolinna sand patch	nil	6·0
TOO 2	as TOO 1	nil	6·1
TOO 3	as TOO 1	nil	6·1
TOO 4	as TOO 1, from area where sand was only a few centimetres deep, overlying calcarenite	tr. (<15)	5·8
TOO 5	as TOO 1	nil	5·8

* 30 gm sand was analysed by volumetric calcimeter technique for calcium carbonate determination. One part soil and two parts (by volume) 1% KC1 were shaken and allowed to stand for one hour before reading pH with a glass electrode and meter. (The pH values obtained using KC1 solution are about 1 unit higher than those obtained from moist soil in the field.)

the Twilight Cove sand patch, were calcareous, analysis of samples from the dune surface at Twilight Cove, and from a pit one metre deep, indicate that the sand contains no calcium carbonate (Table 1). It is possible that the dunes east of Twilight Cove are calcareous, but those being considered here are siliceous to a depth of at least one metre. The sand on the beach at Twilight Cove is also siliceous; in the field the author estimated that there was about 5 per cent calcium carbonate (shell fragments) in the sand.

The sand dunes at Point Culver are probably also siliceous (Parsons 1970); this is suggested by the vegetation recorded on the dunes. Coastal sand deposits at Israelite Bay are mainly siliceous. The deposits on the cliff-top at Toolinna conform to the pattern noted; aeolian calcarenite overlain by unconsolidated siliceous sand. Analysis of the samples from Toolinna showed that there was no calcium carbonate present, though one sample (TOO 4, Table 1) had a trace of calcium carbonate. At Toolinna Cove the sand at the base of the cliffs on the very small beach, underwater, appeared to be siliceous. At the cove the cliffs are not precipitous; there is a modern rockfall allowing access to the base of the cliffs and the small sandy beach.

Lowry (1970) noted a further set of "ancient dunes" on the Hampton Tableland, east of Twilight Cove, composed of siliceous sands. These are probably older than the dunes at Twilight Cove and may date from the middle or early Pleistocene.

While there is only a small amount of geomorphological information available for these areas, certain general features should be noted. The sand deposits along the present shores of the Great Australian Bight show substantial differences in calcium carbonate content. At Israelite Bay, and probably also at Twilight Cove, the sands contain only about 5 per cent calcium carbonate. At Eucla (Fig. 1) and at the Head of the Bight, the sands are composed mainly of calcium carbonate particles, with less than 50 per cent siliceous material (Lowry 1970). At present there is an east-west gradient with higher calcium carbonate levels east of the Roe Plains. The extant cliff-top dunes are composed of siliceous sands. Leaching, by rainwater, of sand dunes containing both siliceous and calcareous grains can result in the complete removal of the calcareous material and the production of pure siliceous sand dunes with an underlying layer of calcarenite. Leaching time depends on many factors, especially climate and the original calcium carbonate levels. Thus the problems associated with these dune systems may be more complex than suggested here.

Finally the very extensive dune systems on the coast of the Bight, associated with the Israelite and Roe Plains, and the Head of the Bight suggest that at times of low sea levels the exposed lowland plain on the continental shelf, south of the Nullarbor Plain, was covered with sand dunes that were continuous across the Bight. The isolated cliff-top dunes reinforce this thesis (J. N. Jennings pers. comm.).

Botanical surveys

Edward John Eyre passed along this part of the Australian coast in 1841 (Eyre 1847). He stopped near Twilight Cove, and then he continued along the cliffs to Point Culver, and eventually reached King George Sound. He certainly traversed the Toolinna and Point Culver dune systems but his comments on the vegetation are very short (Eyre 1847) and he did not collect specimens. In 1870 John Forrest explored the route for an overland telegraph line to link Adelaide and Perth. He travelled along the Israelite Plain to Point Culver, but then he passed inland, keeping about thirty-five kilometres from the coast. He returned to the sea at Twilight Cove. Forrest made useful botanical collections between Israelite Bay and Eucla; he certainly collected south of Point Culver and at Twilight Cove. Some of the specimens were described by Mueller including *Adenanthos forrestii* F. Muell. (Mueller 1882).

The telegraph line, which was surveyed by Forrest was completed in 1877, and some of the telegraph operators who had to live in these very isolated areas, collected plants. Some of the settlers, including John Brooks* of Balbinya (Fig. 2) made observations and collections for Mueller (Brooks 1894, Willis 1959).

Very little attention has been given to this region in recent times, probably due to its inaccessibility. The Israelite Plains have never been examined botanically. George, Beard and Parsons have collected at Twilight Cove, while Wilson and Beard have collected south of Caiguna and near Point Dover. There are no records of collections from Toolinna prior to 1973. The first modern collection of plants from Point Culver was made in October 1973 by M. G. Brooker (pers. comm.) Most of the early collections were sent to Mueller and are lodged in Melbourne (MEL.) Recent collections, including those of the author are lodged in Perth (PERTH), Adelaide (AD) (Parsons 1970), and in Herbarium Australiense, Canberra (CANB). No collections are extant for the Point Dover sand patch.

Vegetation of sand patches and surrounding regions

Parsons (1970) discussed the vegetation of the Twilight Cove dune system in some detail. Apart from a brief comment by Beard (1973) concerning the vegetation of the Israelite Plain, and a similar statement by Brooks (1894), no discussions are available that are relevant to the area (Beard 1973). Willis (1959) described the vegetation of the Nullarbor and Roe Plains at Eucla, about 250 km east of Twilight Cove.

The vegetation of the limestone plateau in the area south of the Eyre Highway (Fig. 2) and between Twilight Cove and Mount Ragged consists mostly of dense mallee scrub, interspersed with clay flats that have a flora dominated by ephemeral plant species (Beard 1973). The scrub is composed of mallee species such as *Eucalyptus cooperana, E. oleosa* and *E. flocktoniae*. There is a sparse understorey of calcicole shrubs such as *Halgania lavandulacea*. Some sclerophyll woodland of taller, non-mallee *Eucalyptus* species occurs in areas to the west of Point Culver and towards the Fraser Range (Beard 1973). The vegetation generally is quite uniform, though variations in these basic types do occur with increasing distance from the coast. The vegetation rarely consists of low tree-less scrub dominated by Chenopodiaceae.

The vegetation of the sand patches is very different from that of the surrounding limestone plateau. At Twilight Cove it consists of very open mallee scrub dominated by *Eucalyptus cooperana, E. foecunda* and several other *Eucalyptus* species (Parsons 1970). *Callitris verrucosa* also is frequent and dominant in a few areas, where aeolian calcarenite is exposed or close to the surface of the sand deposits. The mallee scrub has an understorey of sclerophyllous shrubs. These are mostly from the family Myrtaceae and include several *Melaleuca* species, *Beaufortia empetrifolia* (Parsons 1970), *Calytrix tetragona* and *Darwinia vestita*. In some places members of the Epacridaceae, such as *Conostephium drummondii* and *Lysinema ciliatum* are common. *Adenanthos forrestii** is the only member of the Proteaceae that attains a dominant position in any area; other members of the family are seldom encountered.

On the sand patch at Toolinna, the *Eucalyptus* species are very much less frequent than at Twilight Cove. There is no mallee scrub on the Toolinna dunes, at least in the areas seen by the author. A few very stunted plants of *Eucalyptus incrassata* and *E. diversifolia* were found. The dominant shrubs are species of *Melaleuca*, with frequent occurences of *Acacia cochlearis, Calytrix tetragona* and *Adenanthos forrestii*. The major difference between the vegetation encountered in this area and that at Twilight Cove is the presence here of *Banksia media*. Tall shrubs, up to 5 m, of this species are scattered throughout the dunes.

According to M. G. Brooker (pers. comm.) the vegetation near Point Culver is dominated by mallee *Eucalyptus* species, including *E. diversifolia, E. angulosa* and *E. cooperana. Melaleuca pentagona* is the most prevalent undershrub. Members of the Proteaceae are much more abundant than at Twilight Cove or Toolinna, and *Banksia media* and *B. speciosa* are common (Eyre 1847, M. G. Brooker, pers, comm.). *Grevillea oncogyne* is also abundant.

Beard (1973) indicated that the Israelite Plain probably has a vegetation dominated by *Banksia speciosa;* this being the dominant species on the siliceous sands at Israelite Bay. It should be

* Brooks name is occasionally spelt "Brooke"; an error arising from his signature and style of writing. (Mrs A. E. Crocker, pers. comm., Willis 1959).

* Parsons (1970) listed this species as *Adenanthos sericea* Labill., var. *brevifolia* Benth. His specimen (AD 9682090) was redetermined by the author as *A. forrestii F. Muell.*

Table 2

Species present on dune systems on south-western Nullarbor Plain

Species	Western Australia (see footnote)							S. Aust.	Sand Patches (see footnote)			Species confined to siliceous sands
	i	a	d	w	s	e	E		PC	TO	TC	
Callitris verrucosa (A. Cunn. ex Endl.) F. Muell.							*	*			*	
Amphipogon turbinatus R.Br.		*	*	*	*	*					cf.	*
Danthonia caespitosa Gaudich.								*			*	
Stipa acrociliata Reader							*			cf.	*	
Gahnia lanigera (R.Br.) Benth.						*		*	*	*	*	
Lepidosperma drummondii Benth.				*							*	*
Schoenus lanatus Labill.					(*)					?	*	*
Schoenus nitens (R.Br.) Poir								*			*	
Schoenus pleiostemoneus F. Muell.					*						*	*
Loxocarya flexuosa (R.Br.) Benth.											?	?
Stypandra imbricata R.Br.	*	*					*			*	*	
Tricoryne elatior R.Br.			*					*			*	
Anigozanthos rufa Labill.					*	*			*			*
Casuarina helmsii Ewart & Gordon							*	*	*		*	
Casuarina huegeliana Miq.		*	*		*	*					*	
Casuarina humilis Otto et Dietr.			*	*	*	*				*		*
Adenanthos cuneata Labill.				*	*	*			?	*	*	*
Adenanthos forrestii F. Muell.						*			?	*	*	*
Adenanthos sp. nov.										*		*
Banksia media R.Br.						*			*	*		*
Banksia speciosa R.Br.					*	*			*			*
Conospermum sp.									*			
Grevillea macrostylis F. Muell.						*			*			*
Grevillea oligantha F. Muell.						*				*	*	*
Grevillea oncogyne Diels							*		*			*
Grevillea pinaster Meisn.	*										cf.	*
Grevillea sparsiflora F. Muell.		*							*	*	*	
Hakea cinerea R.Br.						*			*			*
Hakea corymbosa R.Br.					*	*				*		*
Hakea nitida R.Br.						*					*	*
Isopogon trilobus R.Br.					*	*			*		*	*
Petrophile teretifolia R.Br.					*	*			*			*
Stirlingia teretifolia Meisn.						*			*			*
Synaphea cf. *polymorpha* R.Br.			*							*	*	*
Leptomeria pauciflora R.Br.				*	*	*			*			
Rhagodia preissii Moq.		*				*	*	*			*	
Gyrostemon brownii S. Moore							*		*			
Cassytha melantha R.Br.			*		*			*	*	*	*	
Billardiera sp.											sp.	
Acacia cochlearis (Labill.) Wendl.		*	*	*		*				*	*	*
Acacia cyclops A. Cunn. ex G. Don.	*		*			*		*	*			
Acacia erinacea Benth.		*					*	*			*	
Acacia gonophylla Benth.					*	*			*			*
Acacia nitidula Benth.						*			*		cf.	*
Acacia retinodes Schlecht.							*	*			*	
Cassia nemophila Cunn. ex Vog.	*						*	*			*	
Daviesia preissii Meisn.			*			*	*				*	?
Pultenaea obcordata (R.Br.) Benth.						*			*	*	*	*
Sphaerolobium daviesiodes Turcz.					*	*					*	*
Templetonia retusa (Vent.) R.Br.		*	*			*		*	*		*	
Boronia crassifolia Benth.					*	*				*	*	
Correa reflexa (Labill.) Vent.							*	*			*	
Comesperma polygaloides F. Muell.						*	*	*			*	* (granite)
Beyeria leschenaultii (DC.) Baill.		*	*				*	*			*	
Dodonaea stenozyga F. Muell.							*	*	*		*	
Stackhousia scoparia Benth.						*	*	*			*	* (granite)
Cryptandra leucophracta Schlecht.	*	*					*		*	*		*
Cryptandra tomentosa Lindl.		*					*				*	*
Pomaderris myrtilloides Fenzl.						*			*			*
Spyridium denticuliferum Diels					*						*	*
Spyridium spadiceum (Fenzl.) Benth.					*	*					*	*
Spyridium tridentatum (Steud.) Benth.		*	*			*					*	*

Species	Western Australia i	a	d	w	s	e	E	S. Aust.	Sand Patches PC	TO	TC	Species confined to siliceous sands
	(see footnote)								(see footnote)			
Alyogyne hakeifolia (Giord.) Alef.	*	*					*	*	*			
Hibbertia nutans Benth.		*					*				*	?
Hibbertia pungens Benth.		*									*	*
Hibbertia sp.									sp.	sp.		
Pimelea angustifolia R.Br.					*		*		cf.		*	
Pimelea rosea R.Br.		*	*	*	*	*	*		*			*
Pimelea nervosa (Walp.) Meisn.	*	*			*	*	*			*		
Pimelea serpyllifolia R.Br.						*		*			*	
Baeckea sp. aff. *crispiflora* F. Muell									*			
Beaufortia micrantha Schau.						*			*		*	*
Calytrix tetragona Labill.					*	*		*	cp.	*	*	
Chamelaucium axillare F. Muell.						*			*	*		*
Calothamnus gracilis R.Br.					*	*	*			*		*
Darwinia diosmoides (DC.) Benth.		*			*	*	*		*			*
Darwinia vestita (Endl) Benth.					*	*					*	*
Eucalyptus angulosa Schau. (? = *E. incrassata*)					*	*			*		*	
Eucalyptus cooperana F. Muell.						*			*		*	
Eucalyptus diversifolia Bonpl.							*	*	*	*	*	
Eucalyptus foecunda Schau.							*				*	
Eucalyptus eremophila (Diels) Maiden		*			*	*	*		*			
Eucalyptus incrassata Labill.					*	*		*		*	*	?
Eucalyptus scyphocalyx (F. Muell.) Maiden & Blakely							*		*			
Eucalyptus uncinata Turcz.				*					*		*	
Melaleuca elliptica Labill.		*				*	*		*	*		*(granite)
Melaleuca conferta Benth.					*	*					*	?
Melaleuca lanceolata Otto	*		*			*		*	*		*	
Melaleuca pentagona Labill.		*					*		*	*		
Melaleuca pulchella R.Br.						*			*	*		*
Verticordia brownii (Desf.) DC.		*			*	*	*		*			?
Verticordia plumosa (Desf.) Druce			*	*	*	*	*		*			?
cf. *Acrotriche cordata* (Labill.) R.Br.								(*)			*	
Conostephium drummondii (Stschegl.) Gardn.									*		*	(*)
Leucopogon aff. *squarrosus* Benth.											*	(*)
Lysinema ciliatum R.Br.		*	*	*	*	*	*		*	*	*	*
Styphelia hainesii F. Muell.						*					*	
Samolus repens (Forst.) Pers.	*		*	*	*	*	*	*	*	*		
Prostanthera sp.									sp.			
Halgania lavandulacea Endl.						*	*	*			*	
Myoporum insulare R.Br.	*		*		*				cf.		*	
Lechenaultia formosa R.Br.	*	*			*	*				*	*	*
Lechenaultia tubiflora R.Br.		*	*		*	*			*		cf.	*
Scaevola crassifolia Labill.	*		*	*		*		*	*			
Goodenia affinis De Vriese	*	*				*					*	
Goodenia decursiva Fitzg.						*			*			* (granite)
Dampiera parviflora R.Br.						*			*			?
Stylidium pilosum Labill.						*	*		*			*
Calocephalus brownii (Cass.) F. Muell.	*		*	*	*	*		*		*		
Helichrysum obtusifolium F. Muell. & Sond.					*	*		*			*	
Helipterum floribundum DC.				*			*	*			*	
Olearia axillaris (DC.) F. Muell.			*	*		*	*	*	*			

Western Australia: E—Eremean province (Fig. 1); the lower case letters are the initial letter of the zones within the south-west province (Fig. 1) (Beard 1970).

Sand Patch: PC—Point Culver; TO—Toolinna; TC—Twilight Cove (Fig. 2).

sp.—unidentified species present. cf.—specimen collected comparable with species name listed. granite—species associated with granite monadnocks (Beard 1970).

noted that the Toolinna and Twilight Cove sand patches are very lightly vegetated. This contrasts with the very dense scrub that is found west of Israelite Bay.

Species distributions

Species distributions are given in Table 2. The collections from Point Culver (by M. G. Brooker in 1973) and from Toolinna (by E. C. Nelson in 1973) are both incomplete and include only the most frequent or noticeable species, but the Twilight Cove collections are much more extensive. This latter area has been visited several times recently while the two former regions have only been visited once. Despite these inadequacies, the information available is considered sufficient to allow comparisons to be made and conclusions to be reached that are unlikely to be altered significantly by further collections.

The species lists (Table 2) were examined and the species restricted to deep siliceous sand were noted. The distributions of the species

within southern Australia were determined using Black 1922, Eichler 1965 and Beard 1970, and data from the Western Australian Herbarium (PERTH). The distributions of some of the species are discussed below.

(a) Haemodoraceae

Anigozanthos is endemic to the south-west province of Western Australia, where species are found mainly in the siliceous sand plain (Gardner 1973). *Anigozanthos rufa* is the only species that occurs east of Esperance and was previously recorded as far east as Israelite Bay and Mount Ragged. Brooker (pers. comm.) recorded the species on "burnt sandhills, approx. 5 miles north-west of Point Culver about 3-4 miles from the sea". The species is a typical member of the *quonkan*. It has not been found at Toolinna or Twilight Cove and therefore it is not strictly disjunct on the sand patches.

(b) Proteaceae

Both *Banksia* and *Adenanthos* are found in the siliceous sand plain areas west of Israelite Bay, and as far as Shark Bay. The genera are mainly restricted to areas where the soils have little or no calcium, and no species of either genus has been recorded on the Nullarbor Plain in calcareous soils. Neither genus is endemic to Western Australia but none of the species found in south-western Australia occur in south-eastern Australia (Rao 1971).

Banksia speciosa is a very common shrub near Israelite Bay and at Mount Ragged. It was collected by Brooker at Point Culver, thus extending its distribution further to the east. It probably occurs in abundance along the Israelite Plain, but does not reach Toolinna. *Banksia media* was collected at Toolinna and also at Point Culver, but it has never been found at Twilight Cove. Therefore the Toolinna population is the most easterly population of a Western Australian *Banksia* species. *B. media* is common in the *quonkan* between Israelite Bay and Cape Riche (Erickson *et al.*, 1973), and of mallee scrub further inland (J. S. Beard, pers. comm.).

John Eyre stated in his journal for May 1, 1841:

> One circumstance in our route today cheered me greatly, and led me to expect some important and decisive change in the character and formation of the country. It was the appearnce for the first time of the Banksia, a shrub which I have never found to the westward of Spencer's Gulf [South Australia], but which I knew to abound in the vicinity of King George's Sound [Western Australia], and that description of country generally . . . . Isolated as it was amidst the scrub and insignificant as the stunted specimens were that I first met with, they led to an inference that I could not be mistaken in . . . " (Eyre 1847, vol. 2, p. 13-14).

That night (May 1) Eyre probably camped near the Toolinna waterhole (Fig. 2), having already passed through sand patch which is situated northeast of the waterhole. The description of the "stunted specimens" of *Banksia*, fits the habit and form of the plants of *B.media* that were seen recently by the author at Toolinna.

On the succeeding day, Eyre was travelling through the Point Culver sand dunes and he later wrote:

> "We moved through a country which gradually became more scrubby, hilly and sandy . . . . The smaller Banksia [*B. media*] now abounded whilst Banksia grandis, and many other shrubs common at King George's Sound, were frequently met with." (Eyre 1847, vol. 2, p. 14)

The observation that the country became more sandy is exactly what would would be expected in that region; the limestone areas giving way to the dune systems. The increasing prevalence of Western Australian plant species coincides with the situation at Point Culver. Eyre's reference to *Banksia grandis* is incorrect as that species is not commonly found east of King George Sound; the species encountered must have been *B.speciosa*. The most easterly sighting of *Banksia media* is marked on the map published with Eyre's narrative though the position is somewhat inaccurate (Eyre 1847).

Adenanthos species are not as conspicuous as *Banksia*, but they form an important component of the *quonkan* vegetation west of Israelite Bay. *A.cuneata* has been collected at Israelite Bay, Twilight Cove and Mount Ragged (Nelson, in press) and most recently at Toolinna. Brooks collected the species in the late nineteenth century at Israelite Bay, and Batt and Carey collected it at Twilight Cove in 1889 (MEL). The species is abundant at Israelite Bay, but at Toolinna and Twilight Cove it is very rare. Brooker did not collect the species at Point Culver. It is probable that it occurs there today, but it may be rare.

Adenanthos forrestii was first collected by John Forrest (Mueller 1882) on his survey in 1870. Two specimens from his journey are extant (MEL); one is labelled "near Point Culver 33° 14′ S., 124° 2′ E." This location is named 'Wattle Camp' on standard topographic maps and is described by Brooks (1894) as an area of dunes consisting of "very fine sand that has a yellow tint". The second specimen came from the Twilight Cove area. Thus the species was only known from these two areas before its recent collection at Toolinna. It has not been collected at Point Culver, but it could occur there. Forrest's location "near Point Culver" has been misinterpreted in the past and should be regarded now as referring to Wattle Camp, about 36 km south of Point Culver. The species is endemic to these sand patches, and to the Israelite Plain; it is not recorded elsewhere.

A third species of *Adenanthos** was collected at Toolinna in October 1973. It is apparently endemic to that sand patch. It could not be found at Twilight Cove, and no species of *Adenanthos* were collected at Point Culver by Brooker. The possibility that it occurs in these latter areas cannot be ruled out.

* This species has not yet been described. A description is to be published soon by E. C. Nelson in a tanonomic revision of *Adenanthos*.

Among the other members of the family, *Isopogon trilobus* and *Petrophile teretifolia* have been collected at Point Culver, and the former was recently found at Twilight Cove also. Neither species has been collected at Toolinna. *Synaphea cf. polymorpha* was collected at Toolinna and at Twilight Cove. Several species of *Hakea*, including *H.corymbosa* and *H.nitida* were collected at Toolinna and at Point Culver. A number of *Grevillea* species grow at Point Culver, but they have not been recorded on the more easterly sand patches. Most of these species are found in the Israelite Bay and Mount Ragged areas, and like the species of *Adenanthos* and *Banksia* they are restricted to non-calcareous soils. None of these Proteaceae is found on the dunes near the beach at Twilight Cove which contain small amounts of calcium carbonate. The flora of the dunes near the sea, that have some calcium carbonate incorporated, is very different and consists mostly of littoral plants, with occasional *Eucalyptus* and *Melalauca* species.

(c) Myrtaceae

Apart from some significant species of *Eucalyptus* that Parsons (1970) has already discussed, the most significant members of the family that have been recorded on these siliceous dunes are *Chamelaucium axillare, Darwinia vestita* and *D.diosmoides, Calothamnus gracilis, Verticordia brownii* and *V.plumosa*.

Chamelaucium axillare occurs in the *quonkan* between Esperance and Israelite Bay. It has not been collected east of Toolinna, where it was found recently. The genus is endemic to south-western Australia, and is restricted to sand plain areas in that region. *Calothamnus gracilis* is listed by Beard (1970) as occurring in the Eremean Province, but it is usually a sand-plain species (Erickson *et al.* 1973) *Darwinia* and *Verticordia* species fall into similar categories. They are calcifuge species, and while the genera are found in South Australia these species are south-western endemics (Black 1922, Eichler 1965, Beard 1970).

(d) Goodeniaceae

Lechenaultia species are frequent in the *quonkan* west of Mount Ragged. *L.formosa* and *L.tubiflora* have been collected as far east as Twilight Cove, but they are both infrequent on the sand patches. These species are very common near Israelite Bay and are endemic to Western Australia. Some other members of the family recorded on or near the sand patch are calcicoles such as *Scaevola crassifolia* (Parson 1970, N. M. Wace, pers. comm.).

(e) Other families

Other genera recorded on the sand patches but not in the surrounding limestone country include *Pimelea*, *Comesperma* and *Stylidium*. Several different species of *Pimelea* have been recorded on the sand patches, and representatives of the genus are frequent on the younger, coastal sand dunes near Israelite Bay, particularily *Pimelea ferruginea*. *Stylidium pilosum* was collected by Brooker at Point Culver, and it is known from the area between Esperance and Israelite Bay. *Comesperma polygaloides* was collected at Twilight Cove as was *Stackhousia scoparia;* both species found west of Mount Ragged in siliceous sand associated with granite monadnocks (Beard 1970).

The species listed in Table 2 that are restricted to siliceous sand habitats are all endemic to Western Australia. The species that are found either exclusively on limestone or on both siliceous sand and calcareous soils usually occur in south-eastern Australia and in south-western Australia. Thus the flora of these sand patches is composed mainly of Western Australian calcifuge species.

Some of the species had not previously been noted in areas east of Israelite Bay and most of them are absent from the limestone plateau of the Nullarbor Plain. The total species numbers in the sand-patches north-east of Point Culver are very low compared with similar areas west of Israelite Bay; the flora of the sand patches is therefore a depauperate form of the *quonkan* flora typical of the Esperance-Israelite Bay region. However the presence of some of the species at Point Culver indicates that many of the plants may be found on the Israelite Plain, but due to the lack of collections from that area they were not recorded east of Israelite Bay. The flora of the Eyre zone can be said to extend as far as Point Culver, and not to end abruptly at Israelite Bay. It is interesting to note that certain birds which occur in south-western Australia but which previously had not been recorded north-east of Israelite Bay, have recently been seen in the sand-dune at Point Culver, Toolinna and Twilight Cove (See Appendix 1).

There is a gap of about 25 km between Toolinna sand patch and the major dune system at Point Culver. The Point Culver cliff-top dunes are linked to the Israelite Plains by ramps of sand built up by wind against the Wylie Scarp. Similarly between the Toolinna dunes and the second major system at Twilight Cove there is a gap of about 85 km, which is devoid of deposits of siliceous sand apart from the very small sand patch south-west of Point Dover. The areas between the sand dunes are either bare exposed limestone or have clay soils derived from limestone. These intervening areas present no suitable habitats for calcifuge species.

Discussion

These isolated siliceous dune systems are colonised by species which are endemic to Western Australia, and which are considered to be intolerant of soils containing high proportions of calcium. The sand patches are surrounded by an environment which these species are unable to colonise due to the presence of limestone. The

climate, inland from the coast, is apparently unsuitable for the growth of many of these plants; it is characterised by high summer temperatures and low intermittent rainfall.

There are several hypotheses that can be advanced to explain the presence of these species on the sand patches. Firstly, long range dispersal can be considered; plants may have been transported from the areas to the west over the intervening unsuitable habitats by an agency such as wind or animals. Secondly, migration from the west could have occurred when the conditions, both climatic and geomorphic, were suitable in the past. Finally the species could have had a continuous distribution along the coast, but this has since been fragmented (Parsons 1970).

Long range dispersal of plants has been discussed many times. A propagule can probably be dispersed over long distances even if it is not apparently adapted for dispersal by a specific agency such as sea currents, wind or birds (Good 1947). However long range dispersal is only successful if the propagule reaches a habitat that is suitable for its germination and the survival and subsequent reproduction of the plant (Rao 1971). The species that are found on the dune systems east of Point Culver are not obviously adapted for long range dispersal. *Adenanthos* fruits do not appear to be adapted in any way for dispersal over long distances. It is usually difficult to find seeds of *Adenanthos* more than a few metres from a parent plant as the progagules tend to drop directly to the ground on maturity. *Banksia* species also are not adapted for long range dispersal and the same probably applies to the other genera of the Proteaceae and other families. Rao (1971) argued against ocean dispersal of the Proteaceae as the propagules have flimsy coats and are thus susceptible to toxic effects of sea water. Similarly bird dispersal is more probable if species have drupaceous fruits, which none of the species considered here possess (Rao 1971).

It should be noted that many of these species do not have seeds which will germinate readily. In the *quonkan* seedlings of *Adenanthos* species are very rarely found in areas where there are mature plants established. Very occasionally seedlings are encountered in disturbed ground but only if a major disturbance has occurred, such as "bulldozing" or clearing. Seedlings will be found immediately after a fire has burnt the vegetation in an area. This applies equally to other members of the Proteaceae; *Banksia* seeds are usually not released from the fruiting cones until after a fire (Gardner 1959) and they fall directly to the ground. It is unusual to find seedlings among mature communities of *quonkan* vegetation; all plants are apparently of the same age as they probably all germinated after the last fire in the area. In the *Proteaceae* microbial stimulation may be necessary, as seeds will not readily germinate in sterile soils (Rao 1971, Vogts 1960). When these characteristics are considered, along with the lack of adaptation to dispersal over long distances, long range dispersal must be discounted. The extreme sensitivity of many south-western Australian species to changes in edaphic conditions (Diels 1906, Speck 1958) and the very restricted distribution ranges of some species argues strongly in favour of this lack of dispersal capacity.

The second and third hypotheses differ only in their starting points. Parsons (1970) has suggested that disjunctions in the distributions of *Eucalyptus* species can be accounted for simply by postulating a continuous strip of siliceous sand linking the Roe Plains and the areas to the west, during the Quaternary low sea levels. "This would provide continuous species distributions which were subsequently fragmented by rising sea levels" (Parsons 1970).

In assessing this idea it is important to remember that it seems that the species concerned cannot migrate rapidly even over short distances. Thus while there certainly would have been vegetation cover on the exposed coastal lowlands between the Israelite Plains and Twilight Cove, that vegetation is unlikely to have contained all the species typical of the *quonkan*. Rather, only a small proportion of the *quonkan* species may have colonised that coastal area, due to differential migration rates and climatic and edaphic barriers.

In this context it is significant that certain species are not recorded at Twilight Cove, but have been collected in areas to the south-west. A similar situation relates to the Toolinna sand patch. Thus *Banksia speciosa* and *Anigozanthos rufa* are recorded only as far east as Point Culver; they could have reached that dune system by migrating along the existing Israelite Plain. *Banksia media* and *Chamelaucium axillare* are found at Toolinna but not at Twilight Cove. Despite the incomplete collections it is noticeable that the floras of each sand patch becomes poorer in species typical of the *quonkan* the further east they are situated. The Point Culver flora is not as rich in genera and species as that of the Israelite Bay area, and the Toolinna flora is depauperate compared with the Point Culver flora.

This suggests that these species have different capacities to migrate, or if they migrate at the same rate that some species have become extinct from the more easterly dune systems. The latter hypothesis is probably partly correct; due to changes in climate some species may have failed to survive. However, both Frank (1971) and Martin (1973) have indicated that there have not been substantial climatic changes during the late Quaternary in this area. While changes have occurred that have caused vegetation patterns to alter, the climate in the late Pleistocene and Holocene was not very much drier, or wetter, than the climate of the present time (Martin 1973). Thus the climatic effects on the vegetation of these sand dunes may have been small. If different rates of migration are involved, those species that could migrate relatively rapidly reached Twilight Cove, while

those that were slower moving along the exposed coastal plain only reached Toolinna, during the period when sea levels were low.

When marine transgression occurred any plants that had reached Twilight Cove were isolated there and those which were at Toolinna became separated from plants on the other dune system. As mentioned above, the cliff-top dunes were probably emplaced by wind-built ramps situated against the cliffs. The plants would have moved from the exposed coastal plain up these ramps on to the dune systems. Marine erosion has removed these basal ramps, since the sea levels returned to the present datum.

The absence of endemic species on the sand patches, with the probable exception of species of *Synaphea* and *Adenanthos*, indicates that there has been insufficient time for speciation to occur in these isolated populations. The forms of the species that are found on the sand patches are not perceptibly different from phenotypes at Israelite Bay or Mount Ragged. Thus it is probable that the populations at Twilight Cove and Toolinna have only been isolated since the last glacial maximum, and possibly only since the sea levels reached the base of the Baxter Cliffs between 10 000 and 6 000 years B.P. Thom and Chappell 1975; Jennings 1971). It is possible that species which are not potentially very variable, could have been in these areas for longer periods, if the dunes are older than Holocene or late Pleistocene. In the case of *Adenanthos*, the genus is morphologically variable and shows a very substantial amount of phenotypic plasticity, yet forms of the species found on these dunes do not differ significantly from forms found in other areas where those species occur.

It is possible to conclude that the present cliff-top dune systems were probably emplaced in the Holocene, or late Pleistocene, and that the species distribution patterns found in this area have resulted from migrations along a coastal plain during the last period of low sea levels. Subsequent return of sea level to present datum fragmented distributions and isolated species on dune systems disjunct from their main areas of occurrence. Long range dispersal is not thought to account for these disjunctions due to the peculiar propensities of the south-western Australian flora and to the lack of adaptations of their propagules to dispersal over long distances.

One feature of southern Australian phytogeography is the marked difference between the floras of south-eastern and south-western Australia. Several workers have discussed this situation and concluded that species similarities can be accounted for by migrations in post-Tertiary times (Burbidge 1960, Green 1965, Marchant 1973). The Nullarbor Plain limestone plateau is considered to present an edaphic barrier to east-west migrations due to the apparent calcifuge propensity of the Australian vegetation (Crocker and Wood 1947). The flora of south-western Australia exhibits a very high rate of endemism at species level (Beard 1969) and only a very few species that are intolerant of lime-rich environments are found on both sides of the Great Australian Bight.

That only western calcifuge species have reached Twilight Cove is important. Those species that are found both in South Australia and at Twilight Cove (Table 2) are not typically restricted to siliceous sand plain; an example of this category of species is *Eucalyptus diversifolia* (Parsons 1969). It would be expected that an exposed lowland plain, south of the Nullarbor Plain on the continental shelf, would permit migration in *either* direction; to the west or to the east. The absence of eastern calcifuge species demonstrates that either time was not sufficient for such a migration from the east to occur, or that there was a barrier either edaphic or climatic. Migration of these species requires that the exposed plain be composed of siliceous sands. Lowry (1970) noted that between Israelite Bay and Eucla (Fig. 1), the percentage of calcium carbonate in beach sand increased from 5 per cent in the west to about 50 per cent in the east. This may have been the situation in the past, and the higher calcium carbonate levels in eastern areas would have produced an edaphic barrier (Parsons 1970). Further, if calcifuge species were to migrate from the east leaching of the calcareous sands in the east would have to have taken place. A very long time could elapse before a non-calcareous substrate was available for colonisation and migration. One small area of calcareous sand would constitute a very effective barrier to migration. Such a situation would not have prevented calcicole species from migrating from east to west, or *vice versa*, as noted by Parsons (1969). While the prevailing direction of dispersing agencies such as winds and currents, are towards the east, they probably would have had little effect on species migrations unless the species were dispersed by these agencies. As indicated above this is considered unlikely. With only small climatic changes during the Pleistocene period it would appear unlikely that there was a climatic barrier.

The evidence presented here suggests that the duration of periods suitable for migration in the Late Quaternary, or at least during the existence of the extant cliff-top dunes, was insufficient for calcifuge species to migrate across the Great Australian Bight in either direction. Species similarities between the south-eastern and south-western regions of Australia among groups of taxa that have similar propensities to those discussed here, may have resulted from migrations across the exposed continental shelf during the Quaternary. Long range dispersal does not provide a reasonable alternative. If the species disjunctions noted on these cliff-top dunes have resulted from migrations during marine regression in the late Pleistocene, a suitable period for east-west interchange must predate the last period of low sea-levels (120 000-6 000 years B.P.; Chappell 1974).

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Appendix 1: Distribution of birds on south-western Nullarbor Plain

Reilly, Brooker and Johnstone (in press) have recorded the occurrence of species of birds along the coast of the Great Australian Bight, between Point Culver and Twilight Cove. Nine honeyeaters (*Meliphagidae*) were noted, of which two (*Phylidonyris novaehollandiae*—New Holland honeyeater; *Gliciphila melanops*—tawny-crowned honeyeater) were recorded east of their previously known limits of distribution in Western Australia. These two species are

members of the Bassian avifauna of south-western Australia, and were observed only in the vegetation on the siliceous sand deposits. They are probably dependent for food on plants that copiously produce nectar and which are also restricted to those areas, such as species of *Adenanthos*, *Banksia*, *Grevillea* and *Anigozanthos* (Reilly *et al.* in press).

Adenanthos spp., *Anigozanthos rufa*, *Grevillea* spp., and certain other plants are pollinated by nectar-seeking birds. As these plants are found in soils with a very low calcium carbonate content, they probably do not occur east of Twilight Cove and on the limestone areas due to the increased proportions of calcium carbonate in the soils and sand. Survival of populations of these species requires the presence of suitable pollinators. The presence of the honeyeaters in the sand patch vegetation is presumably important with respect to the survival of these disjunct species populations.

The absence of certain honeyeaters from the areas east of Twilight Cove and from limestone areas (Reilly *et al.* in press) may be due to the absence of populations of nectar-producing plants on which those honeyeaters may be dependent.

Reference: Reilly, P. N., Brooker, N. G., Johnstone, G. W., (in press): Birds of the south-western Nullarbor Plain: *Emu*.